

## Phylogenetic Relationships of Geoemydine Turtles (Reptilia: Bataguridae)

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**Abstract:** Monophyly of the batagurid subfamily Geoemydinae was evaluated, and phylogenetic relationships within the subfamily were inferred on the basis of 35 morphological characters. Two approaches, parsimony analysis using the branch and bound algorithm, and neighbor-joining clustering of an absolute distance matrix, were used. The results of these analyses yielded phylograms that were almost identical in branching topology, and poorly supported the monophyly of Geoemydinae. This subfamily thus seems to be a metataxon, most likely consisting of the sister group of Batagurinae (*Geoemyda* group) and a more primitive stock of Bataguridae (*Mauremys* group). The latter accommodates *Mauremys* and *Sacalia* and its monophyly is not well supported. The former consists of the remaining ten geoemydine genera united by two synapomorphies—absence or reduction of the quadratojugal, and posteriorly short-sided anterior neurals. Relationships revealed by our analyses necessitate some changes in the generic classification of Geoemydinae. First of all, *Cistoclemmys* Gray, 1863 (type species: *Ci. flavomarginata*, often synonymized to *Cuora* Gray, 1855 (type species: *Cu. amboinensis*), is shown to be a valid genus closely related to *Pyxidea* and *Geoemyda* rather than to *Cuora* (sensu stricto). *Rhinoclemmys* Fitzinger, 1835 (type species: *R. punctularia*) is shown to be polyphyletic, and *Chelopis* Cope, 1870 (type species: *C. rubida*), is resurrected to accommodate *R. rubida* and *R. annulata*. The plastral hinge seems to have evolved three times in the Bataguridae—in the *Cyclemys*–*Notochelys* clade, *Cuora* (sensu stricto), and the *Cistoclemmys*–*Pyxidea* clade.

**Key words:** Geoemydinae; Bataguridae; Phylogeny; *Geoemyda* group; *Mauremys* group

### INTRODUCTION

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McDowell (1964) recognized three subfamilies, Batagurinae, Emydinae, and Testudininae, in the family Testudinidae. Gaffney and Meylan (1988) raised those

subfamilies to separate families (Bataguridae, Emydidae, and Testudinidae, respectively) of the superfamily Testudinoidea, making the Bataguridae the largest and most divergent family in the order Testudines. They also divided this family into two subfamilies, Batagurinae and Geoemydinae (Gaffney and Meylan, 1988). The former currently contains 22 species of 12 genera (David, 1994; McCord and Iverson, 1994) distributed over most of temperate to tropical Asia, except for the western part (Iverson, 1992). The latter consists of 45 species of 12 genera (David, 1994; McCord et al., 1995, 2000; Fritz et al., 1997; Fritz and Wischuf, 1997; McCord, 1997), occurring in northern Africa, southern Europe, most parts of temperate to tropical Asia, central America, and northern South America (Iverson, 1992).

The first attempt to clarify the phylogeny of the Bataguridae was made by Hirayama (1984) (as the Batagurinae: see above), utilizing cladistic analyses of 37 species representing all recognized genera mainly on the basis of morphological characters. Two major groups were recognized, of which one, consisting of *Batagur*, *Callagur*, *Chinemys*, *Geoclemys*, *Hardella*, *Hieremys*, *Kachuga*, *Malayemys*, *Morenia*, *Ocadia*, *Orlitia*, and *Siebenrockiella*, was characterized by relatively broad triturating surfaces of jaws (=Batagurinae sensu Gaffney and Meylan, 1988), whereas the other, accommodating *Cistoclemmys*, *Cuora*, *Cyclemys*, *Geoemyda*, *Heosemys*, *Mauremys*, *Melanochelys*, *Notochelys*, *Pyxidea*, *Rhinoclemmys* and *Sacalia*, was characterized by relatively narrow triturating surfaces of jaws (=Geoemydinae). Hirayama (1984), while defining the broad triturating surfaces as a synapomorph of the Batagurinae, regarded the narrow triturating surfaces in the Geoemydinae as a primitive condition of the Bataguridae. He thus considered Geoemydinae as paraphyletic, with the *Rhinoclemmys*

*annulata*-*R. rubida*-*Geoemyda*-*Cistoclemmys*-*Pyxidea* clade being monophyletic with the family Testudinidae rather than with the other geoemydine genera. In this hypothesis, the Batagurinae is the sister group of the Geoemydinae plus the Testudinidae, and the Bataguridae is also paraphyletic.

With respect to batagurine monophyly and phylogeny within this subfamily, Gaffney and Meylan (1988) approved Hirayama's (1984) view because most characters Hirayama employed show a low degree of homoplasy in their cladogram. They also shared the view of possible non-monophyly of the Bataguridae with Hirayama, but doubted the geoemydine phylogeny hypothesized by Hirayama because of a very high degree of homoplasy postulated therein. Since then, no comprehensive systematic studies have been carried out for the Bataguridae, leaving both the geoemydine phylogeny and the batagurid monophyly problematic.

Hirayama's (1984) paper was essentially an abstract of a much larger work of character analysis (not yet published), and thus a number of important issues, such as detailed descriptions of character states, were omitted (Gaffney and Meylan, 1988). In addition, a number of taxonomic changes have been made for geoemydine turtles since Hirayama's (1984) analysis (David, 1994; Obst and Reimann, 1994; McCord et al., 1995; Yasukawa et al., 1996; Fritz and Wischuf, 1997; Fritz et al., 1997; Iverson and McCord, 1997a; McCord, 1997; Lehr et al., 1998), though a few recent authors suspect some of these changes to have been misled by artificial hybrids and thus are untenable (van Dijk, 2000; Shi and Parham, 2001; Das, personal communication). These conditions have made it strongly desirable to conduct additional analyses for the geoemydine phylogeny with detailed methodological descriptions and considerations of those taxonomic changes. We therefore analyzed

geoemydine phylogeny on the basis of the morphological characters of 32 species representing 11 genera (i.e., more than 70% of extant species representing all recognized genera but one).

## MATERIALS AND METHODS

Representatives of the following genera were examined (see appendix for further details).

*Cistoclemmys* and *Cuora*.—At present, the genus *Cistoclemmys* Gray, 1863 (type species: *Ci. flavomarginata*), is usually regarded as a junior synonym of *Cuora* Gray, 1856 (type species: *Cu. amboinensis*) (Sites et al., 1984; Ernst and Barbour, 1989; McCord and Iverson, 1991; Iverson, 1992; David, 1994; Fritz and Obst, 1997; Wu et al., 1998). Nevertheless, several authors regard *Cistoclemmys*, also accommodating *Ci. galbinifrons*, as valid (e.g., Bour, 1980; Hirayama, 1984; Gaffney and Meylan, 1988; King and Burke, 1989; Ota, 1991; Zhao and Adler, 1993; Yasukawa and Ota, 1999). We tentatively followed the latter classification because of differences between the two species of *Cistoclemmys* and the remainder of *Cuora sensu lato* (*Cuora sensu stricto*) (Hirayama, 1984; Yasukawa, 1997), and examined the following species as their representatives—*Cistoclemmys flavomarginata* (13 specimens), *Ci. galbinifrons* (7), *Cuora amboinensis* (15), *Cu. aurocapitata* (4), *Cu. mccordi* (6), *Cu. pani* (4), *Cu. trifasciata* (5), and *Cu. zhoui* (4).

Among the five subspecies of *Ci. galbinifrons*, *Ci. g. serrata* is most divergent, exhibiting a weak pair of lateral keels and serration at the posterior margin of the carapace (Fritz and Obst, 1997), whereas the other four subspecies are difficult to distinguish from each other (Iverson and McCord, 1992a; Obst and Reimann, 1994; Lehr et al., 1998). Fritz and Obst (1997) suspected full-species status of *Ci. g. serrata*. Our specimens of *Ci. galbinifrons*

lacked lateral keels or carapace serration (i.e., not belong to *Ci. g. serrata*), but were not identified to subspecies level.

There were no essential differences in characters examined among *Cuora trifasciata*, *Cu. aurocapitata* and *Cu. pani*, although these species differ remarkably from each other in coloration. They are probably very closely related to each other within *Cuora* (McCord and Iverson, 1991). We thus combined them into a single operational taxonomic unit (OTU) as the *Cuora trifasciata* species-group.

*Cyclenys*.—Fritz et al. (1997) described *Cyclenys pulchriata* from Vietnam, and recognized four species, *C. dentata*, *C. oldhamii*, *C. pulchriata*, and *C. tchepouensis*, for this genus mainly on the basis of differences in coloration. On the other hand, Iverson and McCord (1997a), analyzing morphometric variation within *Cyclenys*, described *C. atripons* from southeastern Thailand and Cambodia, and recognized only two species, *C. dentata* and *C. atripons*, for this genus. As such, the taxonomy of *Cyclenys* is still considerably confused, strongly requiring further verification. We examined 14 specimens of *Cyclenys*, but most of them were skeletal specimens and thus were not identified to the species level. Detecting no essential differences in all examined characters, we treated all of them as a single sample, *Cyclenys*, in this analysis.

*Geoemyda*.—This is a name-bearing type genus of the subfamily Geoemydinae. This genus was long regarded as consisting solely of *Geoemyda spengleri*, with two subspecies, *G. s. spengleri* and *G. s. japonica* (e.g., Ernst and Barbour, 1989; Iverson, 1992). Yasukawa et al. (1992), however, elevated both of them to full species, *G. spengleri* and *G. japonica*, because of their remarkable morphological divergences and prominent geographic isolation from each other. Moll et al., (1986), on the basis of comparisons with *G. spengleri sensu lato*, *Heosemys grandis*, and *H. spinosa*, reas-



signed *Heosemys silvatica* to *Geoemyda*. We followed this generic arrangement like a few other recent revisions (David, 1994; McCord et al., 1995; Yasukawa and Ota, 1999).

McCord et al. (1995) also assigned their new species, *Geoemyda yuwonoi*, and the two other species, *Heosemys depressa* and *H. leytenensis*, to *Geoemyda*. However, generic status of the three species remains controversial (Fritz and Obst, 1996; Iverson and McCord, 1997b; Yasukawa and Ota, 1999). Recently, McCord et al. (2000) assigned *G. yuwonoi* to a new genus, *Lencocephalon*, and reassigned *G. depressa* to *Heosemys* on the basis of analysis of mitochondrial DNA variation. Since we did not examine those three species, we tentatively followed McCord et al. (2000). For the genus *Geoemyda* as defined above, *G. japonica* (13), *G. silvatica* (6), and *G. spengleri* (12) were examined.

*Heosemys*.—McDowell (1964) assigned five species, *Heosemys grandis*, *H. spinosa*, *H. depressa*, *G. leytenensis* and *G. silvatica*, to *Heosemys*, probably on the basis of absence of the quadratojugal (squamosal in his terminology). He, however, did not directly examine the latter three species, of which *H. leytenensis* and *H. silvatica* were recently reassigned to *Geoemyda* (see above). We examined *H. grandis* (3) and *H. spinosa* (4).

*Leucocephalon*.—This genus contains only one species, *Leucocephalon yuwonoi*, which was formerly assigned to *Geoemyda* or *Heosemys* (McCord et al., 2000). We have had no chance to examine this species.

*Mauremys*.—This genus currently consists of eight species, *M. annamensis*, *M. caspica*, *M. iversoni*, *M. japonica*, *M. leprosa*, *M. mutica*, *M. pritchardi*, and *M. rivulata* (Fritz and Wischuf, 1997; McCord, 1997), of which six, *M. annamensis* (6), *M. caspica* (1), *M. japonica* (10), *M. leprosa* (2), *M. mutica* (11), and *M. rivulata* (6), were examined. There were no

essential differences in any character among *M. caspica*, *M. leprosa*, and *M. rivulata*. They were formerly considered as three subspecies of *M. caspica*, and are most likely monophyletic (Busack and Ernst, 1980; Ernst and Barbour, 1989; Iverson and McCord, 1994). We thus treat them as constituting a single OTU, the *Mauremys leprosa* species-group.

*Melanocheilus*.—This genus contains two species, *M. tricarinata* and *M. trijuga*, of which only *M. trijuga* (10) was examined.

*Notocheilus*.—We examined six specimens of *N. platynota*, the only representative of this monotypic genus.

*Pyxidea*.—This is a monotypic genus consisting solely of *P. mouhotii*. This species, formerly assigned to *Geoemyda* (e.g., McDowell, 1964) or *Cyclemys* (e.g., Wermuth and Mertens, 1961; Pritchard, 1979), is treated as *Pyxidea* by most recent authors (e.g., Hirayama, 1984; Ernst and Barbour, 1989; Iverson, 1992; David, 1994). Five specimens were examined.

*Rhinoclemmys*.—This is the only batagurid genus occurring in central and South America, and includes nine species: *annulata*, *areolata*, *diademata*, *funerea*, *melanosterna*, *nasuta*, *pulcherrima*, *punctularia*, and *rubida* (David 1994). Hirayama (1984) suggested the polyphyly of the genus, but all subsequent authors have apparently ignored this account (e.g., Ernst and Barbour, 1989; Iverson, 1992; David, 1994). Therefore, we tentatively treated them as composing a single genus, and examined *R. annulata* (2), *R. areolata* (2), *R. funerea* (3), *R. pulcherrima*, (5), *R. punctularia* (4), and *R. rubida* (1).

*Sacalia*.—Iverson and McCord (1992b) recognized three species, *S. bealei*, *S. quadriocellata*, and *S. pseudocellata*, for this genus. They showed some differences in coloration and shell shape, but none in internal morphology. We examined *S. bealei* (2), *S. quadriocellata* (2), and *Sacalia* sp. (2: skeletal specimens not identified at



the species level). Because no essential differences existed among these specimens in any character, we treat them as a single OTU, *Sacalia*.

**Batagurinae.**—To evaluate states of characters in ingroup taxa and test their monophyly, we examined 44 batagurine specimens of 12 species representing all of the currently recognized batagurine genera: *Batagur baska* (2 specimens), *Callagur borneoensis* (3), *Chinemys reevesii* (10), *Geoclemys hamiltonii* (2), *Hardella thurjii* (3), *Hieremys annandalii* (3), *Kachuga smithii* (5), *Malayemys subtrijuga* (4), *Morenia petersi* (2), *Ocadia sinensis* (4), *Orlitia borneensis* (1), and *Siebenrockiella crassicollis* (5) (see "Specimens Examined" for further details). Das (2001) divided the genus *Kachuga* and assigned *K. smithii* and other three congeneric species to a separate genus, *Pangshura* Gray, 1869, usually regarded as a junior synonym or a subgenus of *Kachuga* (Wermuth and Mertens, 1977; Moll, 1987). However, we tentatively treated the two genera as a single unit, genus *Kachuga*, because both genera are possibly valid but probably monophyletic (Hirayama, 1984; Moll, 1987). In the "Characters Examined and Distribution of Their States" section, we refer to these species only by their generic name. We selected two batagurine genera, *Orlitia* and *Siebenrockiella*, as the possibly closest outgroup of the Geoemydinae, because these genera exhibited a particular similarity, as batagurines, with the latter by having narrow, ridgeless triturating surfaces, and lacking the secondary palate. *Orlitia* and *Siebenrockiella*, possibly closely related to each other, are likely to be regarded as the most primitive batagurines (McDowell, 1964; Carr and Bickham, 1986; Hirayama, 1984; Gaffney and Meylan, 1988).

We analyzed 35 characters: 20 for the skull, one for the hyoid apparatus, ten for the shell, one for the pelvic girdle, and three for soft parts). Several characters

employed by McDowell (1964) and Hirayama (1984) were not used in our analyses, because they showed high intraspecific and/or intrageneric variation in ingroup taxa. These characters include: the shape of the fissura ethmoidalis, scutellation of the forearm, web of the hindlimb digits, and subdivision of the foramen nervi trigeminalis. See "Characters Examined and Distribution of Their States" for further details.

A species-character state matrix (Table 1) was analyzed using the Branch and Bound algorithm of PAUP (version 3.1.1., Swofford, 1991) to find all parsimonious networks, which were rooted by the outgroup species. All characters were set as ordered condition and were equally weighted. Three kinds of indices, consistency index (Kluge and Farris, 1969), retention index (Farris, 1989a), and rescaled consistency index (Farris, 1989b), were calculated for goodness-of-fit statistics.

In addition, we applied a neighbor-joining method (Saitou and Nei, 1987) for an absolute distance matrix using the NEIGHBOR program in PHYLIP (version 3.5c, Felsenstein, 1989) following Hikida (1993). The network calculated was also rooted by the outgroup species. This analysis was aimed at evaluating the validity of the relationships proposed in parsimonious trees and to assess the degrees of differentiation among samples. Since all characters were set as ordered condition in this study, the absolute distance ( $\text{diff}(y, z)$ ) was calculated as  $\text{diff}(y, z) = y - z$  following Swofford (1991). The resultant absolute distance matrix is given in Table 2.

#### CHARACTERS EXAMINED AND DISTRIBUTION OF THEIR STATES

We examined states of 35 characters as below for our 26 geoemydine and 12 batagurine samples (Table 1).

**Characters Used for the Phylogenetic Analysis**

TABLE 1. Species-character state matrix for the subfamily Geoemydinae and its relatives.

Samples	Characters																																						
	1										2										3																		
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5				
Geoemydinae																																							
<i>Cistoclemmys flavomarginata</i>	0	2	1	1	1	1	?	?	2	0	0	1	1	1	0	0	2	2	0	1	2	2	0	0	1	1	1	2	2	1	1	0	0	1	0				
<i>Cistoclemmys galbinifrons</i>	0	1	1	1	0	0	1	1	1	0	0	1	1	0	1	0	0	1	0	1	2	2	0	0	1	1	1	2	2	1	1	0	0	1	0				
<i>Cuora amboinensis</i>	1	0	0	0	0	0	1	1	1	0	1	0	0	2	2	0	0	2	1	0	2	2	0	0	1	1	0	2	2	1	1	0	0	0					
<i>Cuora mccordi</i>	0	0	0	0	0	0	1	1	2	0	0	0	0	2	2	1	0	2	1	0	1	1	0	0	1	0	0	2	2	1	1	0	0	0					
<i>Cuora trifasciata</i> species group	0	0	0	0	0	0	1	1	2	0	0	0	0	2	2	1	0	2	1	0	1	0	0	0	1	0	0	2	2	1	1	0	0	0					
<i>Cuora zhoui</i>	0	0	0	0	0	0	1	1	2	0	0	0	0	2	2	0	0	2	1	0	1	0	0	0	1	0	0	2	2	1	1	0	0	0					
<i>Cyclemys</i> spp.	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	2	1	2	0	1	0	0			
<i>Geoemyda japonica</i>	0	2	2	1	1	0	1	0	2	1	0	1	1	0	2	0	1	2	0	1	0	0	1	1	1	0	1	1	1	1	1	0	1	0					
<i>Geoemyda silvatica</i>	0	1	1	1	1	1	?	?	2	1	0	1	1	0	1	0	2	0	0	1	0	0	0	1	1	0	1	1	1	1	0	0	1	0					
<i>Geoemyda spengleri</i>	0	2	2	1	1	0	0	2	1	0	1	1	0	2	0	1	1	0	1	0	0	1	1	1	0	1	1	1	1	1	0	1	0						
<i>Hepsemys grandis</i>	2	0	0	0	0	1	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0	1	0	0			
<i>Heosemys spinosa</i>	0	0	0	0	0	1	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0	1	0	0			
<i>Mauremys annamensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Mauremys japonica</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Mauremys leprosa</i> species group	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Mauremys mutica</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Notochelys platynota</i>	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	2	1	2	0	0	0	0		
<i>Melanochelys trijuga</i>	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Pyxidea mouhotii</i>	0	2	1	1	1	0	1	1	2	0	0	1	1	0	0	0	0	2	0	1	1	0	1	1	1	0	1	2	1	1	0	0	0	0					
<i>Rhinoclemmys annulata</i>	0	0	0	0	0	0	1	1	2	0	1	0	1	1	1	0	0	2	0	1	0	0	0	0	1	0	0	1	1	1	1	0	0	0					
<i>Rhinoclemmys areolata</i>	0	0	0	0	0	0	1	0	0	0	1	0	0	2	2	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Rhinoclemmys funerea</i>	1	0	0	0	0	1	0	0	0	1	0	0	2	2	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Rhinoclemmys pulcherrima</i>	1	0	0	0	0	1	0	0	0	1	0	0	2	2	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Rhinoclemmys punctularia</i>	2	0	0	0	0	1	0	0	0	1	0	0	2	2	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Rhinoclemmys rubida</i>	0	0	0	0	0	0	1	1	2	0	0	0	1	0	2	0	0	2	0	1	0	0	0	0	1	1	0	1	1	1	1	0	0	0					
<i>Sacalia</i> spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
Batagurinae																																							
<i>Orlitia borneensi</i>	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Siebenrockiella crassicollis</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		

1. Frontal exposure onto orbital rim

In *Chinemys*, *Hieremys*, *Malayemys*, *Morenia*, and *Orlitia* of the batagurines, and *Heosemys grandis* and *Rhinoclemmys punctularia* of the geoemydines, the frontal was separated from the orbital rim by a strong connection between the prefrontal and postorbital. This condition was some-

times observed in *Siebenrockiella*, *Rhinoclemmys pulcherrima*, *R. funerea*, and *Cuora amboinensis*. In the other species, the frontal usually reached the orbital rim, but was sometimes separated by a very weak connection. We coded this character as: (0) usually present, without prefrontal-postorbital connection; (1) sometimes

TABLE 2. Absolute distance matrix for species of the subfamily Geoemydinae and its relatives.

Samples	Characters																										
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
1 <i>Cistoclemmys flavomarginata</i>																											
2 <i>Cistoclemmys galbinifrons</i>	9																										
3 <i>Cuora amboinensis</i>	2015																										
4 <i>Cuora naccordi</i>	2118	7																									
5 <i>Cuora trifasciata</i> species-group	2219	8	1																								
6 <i>Cuora zhoii</i>	2118	7	2	1																							
7 <i>Cyclemys</i> spp.	2720	1916	1514																								
8 <i>Geoemyda japonica</i>	1820	2924	2322	26																							
9 <i>Geoemyda silvatica</i>	1817	3025	2423	21	8																						
10 <i>Geoemyda spengleri</i>	1920	3126	2524	26	2	7																					
11 <i>Hepsemys grandis</i>	3025	2221	2019	726	2025																						
12 <i>Heosemys spinosa</i>	2823	2219	1817	524	1823	2																					
13 <i>Mauremys annamensis</i>	2924	1916	1514	1424	2122	1311																					
14 <i>Mauremys japonica</i>	2621	1815	1413	1121	1819	10	8	5																			
15 <i>Mauremys leprosa</i> species-group	2621	1815	1413	1123	1821	10	8	3	2																		
16 <i>Mauremys mutica</i>	2722	1714	1312	1222	1920	11	9	2	3	1																	
17 <i>Melanochelys trijuga</i>	2619	1613	1211	919	1621	10	8	11	10	8	9																
18 <i>Notochelys platynota</i>	2720	1916	1514	2262	126	9	7	12	9	9	10	9															
19 <i>Pyxidea mouhotii</i>	1213	2419	1817	1711	1213	2220	2722	2425	1617																		
20 <i>Rhinoclemmys annulata</i>	2017	1411	10	915	1716	1916	1413	1010	11	815	16																
21 <i>Rhinoclemmys areolata</i>	2622	1110	9	814	2022	2214	12	8	9	7	6	714	23	7													
22 <i>Rhinoclemmys funerea</i>	2925	1213	1211	1523	2525	1515	1112	10	910	1526	10	3															
23 <i>Rhinoclemmys pulcherrima</i>	2723	1011	10	915	2123	2313	13	910	8	7	815	24	8	1	2												
24 <i>Rhinoclemmys punctularia</i>	3026	1314	1312	1624	2626	1416	1213	1110	1116	2711	4	1	3														
25 <i>Rhinoclemmys rubida</i>	2015	1411	10	915	1516	1716	1413	1212	11	815	16	4	912	1013													
26 <i>Sacalia</i> spp.	2621	2017	1615	923	1821	8	6	5	4	2	3	8	722	12	912	1013	12										
27 <i>Orlitia borneensis</i>	2924	2322	2120	1226	1924	7	9	8	9	7	811	1023	1714	1513	1417	5											
28 <i>Siebenrockiella crassicollis</i>	3025	2423	2221	1125	2023	8	8	7	8	8	912	922	1815	1614	1718	6	3										

absent, with weak prefrontal-postorbital connection; (2) absent, with strong prefrontal-postorbital connection.

2. *Processus inferior parietalis*

The right and left processus inferior parietalis were almost parallel in most batagurids. In *Cistoclemmys flavomarginata*, *Geoemyda japonica*, *G. spengleri*, and *Pyxidea*, the processus were close to each other ventromedially, and the lower part of the cranial cavity was strongly convergent.

*Cistoclemmys galbinifrons* and *Geoemyda silvatica* had the cranial cavity weakly convergent ventrally. We coded this character as: (0) almost parallel; (1) weakly approximating; (2) approximating.

3. *Foramen nervi viduani*

The foramen nervi viduani was located anteriorly to the anteroventral part of the processus inferior parietalis, and was bordered by the processus and palatine in most batagurid species. In *Geoemyda*,



*Hardella*, *Morenia*, *Cistoclemmys*, *Geoemyda*, and *Pyxidea*, the foramen was located posterolaterally or laterally to the anteroventral part of the processus inferior parietalis, bordered by the parietal, pterygoid, and epipterygoid, or sometimes open in the pterygoid (2/3 of *Geoemyda japonica* and 3/5 of *G. spengleri*). We coded this character as: (0) bordered by processus inferior parietal and palatine; (1) bordered by parietalis, pterygoid, and epipterygoid; (2) usually on pterygoid.

#### 4. Medial process of jugal

In most batagurid species, the medial process of the jugal was moderately to well developed, and its ventromedial tip was expanded. In *Cistoclemmys*, *Geoemyda*, and *Pyxidea*, the process was weak and had a tapering ventromedial tip. We coded this character as: (0) moderate to well developed; (1) weak.

#### 5. Contact between jugal and pterygoid

Most batagurid species had a medial process of the jugal which was firmly connected with the pterygoid. In *Cistoclemmys flavomarginata*, *Geoemyda*, and *Pyxidea*, the connection was usually absent or very weak if present. We coded this character as: (0) present; (1) usually absent or very weak.

#### 6. Quadratojugal

Among batagurines, *Callagur*, *Batagur*, *Chinemys*, *Geoclemmys*, *Hardella*, *Malayemys*, and *Orlitia* had a massive quadratojugal, whereas in *Kachuga*, *Morenia*, *Ocadia*, and *Siebenrockiella* the quadratojugal was small to moderate in size. On the other hand, most geoemydines had a much smaller quadratojugal, although this element was moderate in size in *Mauremys* and *Sacalia*, and was exceptionally elongated but laterally strongly compressed in *Geoemyda spengleri*. *Hieremys*, *Cistoclemmys flavomarginata*, *Geoemyda silvatica*, and *Heosemys*

had no quadratojugal at all. We coded this character as: (0) present; (1) absent.

#### 7. Contact between quadratojugal and squamosal

In batagurines exclusive of *Hieremys*, the quadratojugal was firmly connected to the squamosal as well as to the quadrate and the jugal. On the other hand, the quadratojugal was absent (see above), or if present, did not usually contact the squamosal in most geoemydines. In *Geoemyda spengleri*, *Mauremys* and *Sacalia*, however, a weak contact was usually present. We coded this character as: (0) usually present; (1) absent; (?) no quadratojugal.

#### 8. Contact between jugal and quadratojugal

The contact between the jugal and the quadratojugal was present in batagurines except for *Hieremys*, while it was usually absent in the geoemydines. A weak contact was present in *Geoemyda japonica*, *G. spengleri*, *Mauremys*, *Rhinoclemmys areolata*, *R. funerea*, *R. pulcherrima*, *R. punctularia*, and *Sacalia*. We coded this character as: (0) present; (1) absent; (?) no quadratojugal.

#### 9. Bony beak of upper jaw

Most batagurid turtles had a shallow notch on the anteroventral margin of the unhooked bony beak composing the upper jaw. The corresponding portion was usually flat, or sometimes only weakly notched, with or without making the anterior portion hook-shaped as a whole, in *Kachuga*, *Cuora amboinensis*, *Cistoclemmys galbinifrons*, and *Mauremys japonica*. In *Cistoclemmys flavomarginata*, *Cuora* exclusive of *Cu. amboinensis*, *Geoemyda*, *Pyxidea*, *Rhinoclemmys annulata*, and *R. rubida*, the beak was unnotched and, slightly but distinctly hooked. We coded this character as: (0) notched and unhooked; (1) usually flat, but sometimes with a very weak notch or hook; (2) unnotched and distinctly hooked.

*10. Ventromedial meeting of maxillae at bony beak of upper jaw*

In most batagurid genera, the tip of the bony beak of the upper jaw was formed by the premaxilla, sometimes with very weak participation of the maxilla. In *Geoemyda*, the right and left maxillae were firmly connected ventromedially with each other, forming the beak. We coded this character as: (0) absent or sometimes present but very weak; (1) present.

*11. Serration of upper labial margin of maxilla*

*Batagur*, *Callagur*, *Hardella*, *Kachuga*, *Morenia*, and *Ocadia* of the batagurines had moderate to strong serration at the upper labial margin of the maxilla, whereas the other batagurines and most geoemydines did not have such serration. *Rhinoclemmys* species except for *R. rubida* had the serration weaker than in the above mentioned batagurines. We coded this character as: (0) absent; (1) present.

*12. Size and shape of foramen palatinum posterius*

The foramen palatinum posterius was small and round in *Cistoclemmys*, *Geoemyda*, and *Pyxidea*, as well as in the batagurines. On the other hand, the foramen was large, and elliptic or oval, about two times longer than wide, in the other geoemydines. We coded this character as: (0) large, and elliptic or oval; (1) small and round.

*13. Anteromedial portion of upper triturating surface*

In *Orlitia* and *Siebenrockiella*, and most geoemydines, the anteromedial portion of the upper triturating surface was narrower than the posterior portion, and the posteroventral portion of the premaxilla was excluded from the surface. In *Cistoclemmys*, *Geoemyda*, *Pyxidea*, *Rhinoclemmys*

*annulata*, and *R. rubida*, the anteromedial portion of the upper triturating surface was expanded medially and broader than the posterior portion, and the posteroventral portion of the premaxillae participated in the triturating surface. This character state was usually observed in the batagurines except for *Orlitia* and *Siebenrockiella*. The posterior triturating surface was very narrow in *Cistoclemmys*, *Geoemyda*, *Pyxidea*, *R. annulata* and *R. rubida*, whereas it was broad in batagurines. We coded this character as: (0) narrower than posterior portion; (1) relatively narrow but expanding medially; (2) broad and expanding medially.

*14. Contact between maxilla and vomer*

A firm connection between the maxilla and vomer usually existed in most batagurid species. On the other hand, the contact was absent in *Cuora*, *Rhinoclemmys areolata*, *R. funerea*, *R. pulcherrima*, and *R. punctularia*, and it was very weak or sometimes absent in *Cistoclemmys flavomarginata*, *Mauremys*, and *Rhinoclemmys annulata*. We coded this character as: (0) present; (1) very weak, sometimes absent; (2) absent.

*15. Position of foramen praepalatium*

In *Cistoclemmys flavomarginata*, *Cyclemys*, *Heosemys*, *Notochelys*, *Pyxidea*, and *Sacalia*, as well as in all batagurines, the foramen praepalatium was located between the premaxilla and the vomer. In contrast, the foramen opened within the premaxilla in *Cuora*, *Geoemyda japonica*, *G. spengleri*, *Mauremys annamensis*, *M. mutica*, and *Rhinoclemmys* except for *R. annulata*. In the other geoemydines, the foramen was usually located near the suture between the premaxilla and vomer, or sometimes within the premaxilla. We coded this character as: (0) between premaxilla and vomer; (1) sometimes within premaxilla; (2) within premaxilla.

### 16. Notch of prefrontal at posterior orbital margin

The prefrontal was usually shallowly notched at the posterior orbital margin in the *Cuora trifasciata* species-group and *Cu. mccordi*. Such a notch was absent in the other species. We coded this character as: (0) absent; (1) mostly present.

### 17. Contact between maxilla and pterygoid

The maxilla contacted the pterygoid in most batagurid species. On the other hand, such a contact was absent in *Cistoclemmys flavomarginata*, and was very weak or sometimes absent in *Geoemyda*. We coded this character as: (0) present; (1) very weak or sometimes absent; (2) absent.

### 18. Prootic participation in processus trochlearis oticum

*Cyclemys*, *Geoemyda silvatica*, *Heosemys*, *Mauremys*, *Notochelys* and *Sacalia*, as well as batagurines, had the processus trochlearis oticum mainly formed by the prootic. In *Cistoclemmys flavomarginata*, *Cuora*, *Geoemyda japonica*, *Melanochelys*, *Pyxidea*, and *Rhinoclemmys*, the prootic exposure was distinctly reduced, with the processus mainly formed by the quadrate. In the other geoemydines, the processus was formed by both prootic and quadrate. We coded this character as: (0) mainly by prootic; (1) by both prootic and quadrate; (2) mainly by quadrate.

### 19. Quadrate participation in canalis cavernosum

The quadrate participated in the canalis cavernosum in *Cuora*, while it usually did not in the remaining batagurids. We coded this character as: (0) absent; (1) usually present.

### 20. Hyoid apparatus

In most batagurid turtles, the hyoid was well ossified, and the second pair of branchial horns was slightly shorter than the

first. On the other hand, the hyoid was weakly ossified (rather cartilaginous), and the second pair was much shorter than the first in *Cistoclemmys*, *Geoemyda*, *Pyxidea*, *Rhinoclemmys annulata*, and *R. rubida*. We coded this character as: (0) well ossified with second branchial horns slightly shorter than the first; (1) weakly ossified with second branchial horns much shorter than the first.

### 21. Plastral hinge

The plastral hinge was present in *Cistoclemmys*, *Cuora*, *Cyclemys*, *Notochelys*, and *Pyxidea*. They also possessed a well to extensively developed musculus testoscapularis and m. testoiiliacus, which were associated with shell closure (Bramble, 1974). Among them, only *Cuora amboinensis* and *Cistoclemmys* closed both anterior and posterior plastral lobes without gaps between the carapace and plastron. We did not examine the condition of the muscles in *Batagur* and *Geoclemmys*, which lack a plastral hinge. The other species lacked a plastral hinge and m. testoscapularis and m. testoiiliacus were poorly developed. We coded this character as: (0) absent; (1) present but impossible to close without gaps; (2) present and possible to close without gaps.

### 22. Anal notch of plastron

The plastron was distinctly notched posteromedially at the anal scutes in most batagurids. However, the notch was very shallow in *Cuora mccordi*, and absent in *Cistoclemmys*, and *Cuora amboinensis*. We coded this character as: (0) present; (1) present but very shallow; (2) absent.

### 23. Serration at posterior margin of carapace

*Hieremys*, *Siebenrockiella*, *Cyclemys*, *Geoemyda japonica*, *G. spengleri*, *Heosemys*, *Mauremys japonica*, *Notochelys*, and *Pyxidea* had strong serration at the posterior margin of carapace. In the other



species, the serration was absent or weakly developed only in young individuals. We coded this character as: (0) absent, or weak and only in young individuals; (1) strong.

#### 24. Longitudinal keels on carapace

*Chinemys*, *Geoclemys* and *Malayemys* of batagurines, and *Geoemyda*, *Melanochelys*, and *Pyxidea* of the geoemydines had three longitudinal rows of strong keels on the carapace with distinct ridges on the bony plates. In the other batagurid species, only the medial keel was usually developed: the lateral keels were absent or, if present, very weak without distinct ridges on the bony plates. We coded this character as: (0) weak, usually in a single row; (1) prominent, in three rows.

#### 25. Anterior part of neural bones

In *Hieremys* of the batagurines and the geoemydines exclusive of *Mauremys*, *Sacalia*, and *Notochelys*, the anterior neurals were usually hexagonal with posterior sides shorter than anterior sides. In the other species, the neurals were also usually hexagonal but the anterior sides were shorter than the posterior sides. We coded this character as: (0) short-sided anteriorly; (1) short-sided posteriorly.

#### 26. Sutures between lateral sides of seventh and eighth pleurals

In most batagurids, the seventh and eighth pleurals on each side were separated by the eighth neural and the anterior suprapyg. In *Cistoclemmys*, *Cuora amboinensis*, and *Rhinoclemmys rubida*, the eighth neural and the anterior suprapyg were usually absent, and the lateral sides of seventh and eighth pleurals were sutured with each other. We coded this character as: (0) absent; (1) present.

#### 27. Cloacal bursae

The cloacal bursae were present in most batagurids, while it was much reduced or completely lost in *Cistoclemmys*, *Pyxidea*,

and *Geoemyda*. We could not examine the condition of this character in *Batagur* and *Geoclemmys*. We coded this character as: (0) present; (1) much reduced or lost.

#### 28. Axillary plastral buttress

In *Chinemys*, *Hieremys*, and *Morenia* of the batagurines, and in most geoemydines having no plastral hinge, the dorsal portion of the axillary plastral buttress was connected around the portion between the peripherals and the costals, and the connected portion was distinctly concave. In all geoemydines having a plastral hinge (*Cyclemys*, *Notochelys*, *Cuora*, *Cistoclemmys*, and *Pyxidea*: see above) the dorsal portion of the buttress was very short and connected to the peripherals, and the connected portion was not or only scarcely concave. In *Mauremys annamensis* of the geoemydines, and in *Geoclemys*, *Malayemys*, *Orlitia*, and *Siebenrockiella* of the batagurines, the dorsal portion of the buttress was long, expanded, and strongly connected to the costals, and the connected portion was distinctly concave. In the other batagurines, the buttress was much more developed than in *M. annamensis*, *Malayemys*, *Orlitia*, and *Siebenrockiella*, and was very strongly connected to the costals, almost reaching the ribs. We coded this character as: (0) very strongly connected to costals, almost reaching ribs; (1) strongly connected to costals; (2) connected around the portion between peripherals and costals; (3) weakly connected to the peripherals.

#### 29. Inguinal plastral buttress

In *Chinemys*, *Malayemys*, *Morenia*, and *Orlitia* of the batagurines, and most geoemydines, the dorsal portion of inguinal plastral buttress was connected around the suture between the peripherals and the costals, and the connected portion was distinctly concave. In *Mauremys annamensis*, *Geoclemys*, and *Siebenrockiella*, the dorsal portion of the

buttress was long, expanded, and strongly connected to the costals, and the connected portion was distinctly concave. In *Hieremys*, *Cistoclemmys*, *Cuora*, and *Pyxidea*, the dorsal portion was very short, and the connected portion was not concave. In the other batagurines, the buttress was strongly developed, almost touching the rib. We coded this character in the same way as Character 28.

### 30. Internal choanae

Parsons (1960) examined the structure of the choanae for most batagurids. We followed his terminology for the structure. Our examination revealed that *Chinemys*, *Hieremys*, *Ocadia*, *Orlitia*, and *Siebenrockiella* of batagurines, and most geoemydines had the internal choanae with a flap or a ridge. Some specimens of *Mauremys mutica*, *Rhinoclemmys pulcherrima*, and *Cistoclemmys flavomarginata* had the internal choanae with a very weak flap, resembling a ridge. In *Mauremys rivulata*, *M. mutica*, *Melanochelys*, and *Rhinoclemmys pulcherrima*, some specimens had a flap and others had a ridge. The internal choanae had a small papilla in *Callagur*, *Hardella*, *Kachuga*, *Morenia*, 2/4 of *Notochelys*, *Cyclemys*, *Rhinoclemmys funerea*, and *R. punctularia*. The internal choanae lacked a papilla, flap, or ridge in *Malayemys* and *Heosemys*. We could not examine this character state in *Batagur* and *Geoclemys*. We coded this character as: (0) without papilla, flap, or ridge; (1) with flap or ridge; (2) usually with papilla.

### 31. Skin of posterior head

The skin of the posterior head was smooth in most geoemydines, but subdivided into small scales in *Cyclemys*, *Geoemyda silvatica*, *Heosemys*, *Melanochelys*, *Notochelys*, and *Pyxidea* of the geoemydines, as well as in the batagurines. We coded this character as: (0) subdivided into small scales; (1) smooth.

### 32. Radiated markings on plastron

Radiated markings were observed on each plastral scute in *Cyclemys* and *Heosemys*. We coded this character as: (0) absent; (1) present.

### 33. Entoplastron

In turtle taxonomy, many authors paid attention to whether the entoplastron was intersected by the humero-pectoral seam (e.g., Boulenger, 1889; Smith, 1931; Bourret, 1941; Pritchard, 1979; Ernst and Barbour, 1989). Our examination revealed that among batagurines, the state of this character was variable, seemingly reflecting the phylogeny (Hirayama, 1984). On the other hand, the entoplastron was consistently intersected by the seam in all the geoemydines but *Geoemyda silvatica*. Therefore, the absence or presence of the intersection was not informative for the inference of geoemydine phylogeny. In the specimens of *G. silvatica* examined by us, the entoplastron was intersected by the seam near the posterior rim (4/5) or overlapped by the seam at the posterior rim (1/5). We thus considered that the absence of the intersection represented rather minor individual variation in this species, although Moll et al. (1986) reported the absence of intersection of entoplastron by the humero-pectoral seam in this species.

We also examined whether the entoplastron was intersected by the gulo-humeral seam. In most batagurid species, the entoplastron was intersected by this seam or barely separated from it (1/10 of *M. mutica* and 2/9 of *Sacalia*), but in *Geoemyda* the entoplastron was in a separate location posterior to the gulo-humeral seam. We coded the character as: (0) entoplastron mostly intersected by gulo-humeral seam; (1) entoplastron separated from gulo-humeral seam.

### 34. Antero-dorsal portion of iliac blade

In most batagurids, the antero-dorsal portion of the iliac blade was about as

long as its postero-dorsal portion (Fig. 1b, e–j). Only in *Cistoclemmys*, the antero-dorsal portion was about two times longer than the postero-dorsal portion (Fig. 1c, d). We coded this character as: (0) as long as its postero-dorsal portion; (1) two times longer than its postero-dorsal portion.

**35. Small foramen on ventral maxilla**  
*Rhinoclemmys funerea* and *R. punctularia* usually had a very small foramen on the ventromedial portion of the maxilla. Such a foramen was absent in the remaining batagurids. We coded this character as: (0) absent; (1) usually present.

RESULTS

All characters examined were informative for the inference of relationships among the 26 geoemydine OTUs.

Three equally parsimonious trees (tree length=107; consistency index (CI)=0.449; retention index=0.762; rescaled consistency index=0.342) were detected. *Mauremys japonica*, the *M. leprosa* species-group, and the *M. annamensis*–*M. mutica* clade were trifurcated in all trees. These trees differed from each other in topology involving *Rhinoclemmys annulata*, *R. rubida*, and the *Geoemyda*–*Cistoclemmys*–*Pyxidea* clade. In the strict consensus tree (Fig. 3), therefore, their relationships were also expressed as trifurcated.

The consistency index for these data was low (CI=0.449). However, this index is known to be highly negatively correlated with numbers of OTUs included in an analysis (Sanderson and Donoghue, 1989; Klassen et al., 1991). Our analysis involved a relatively large number of OTUs (28), and the value, while being similar to that in a

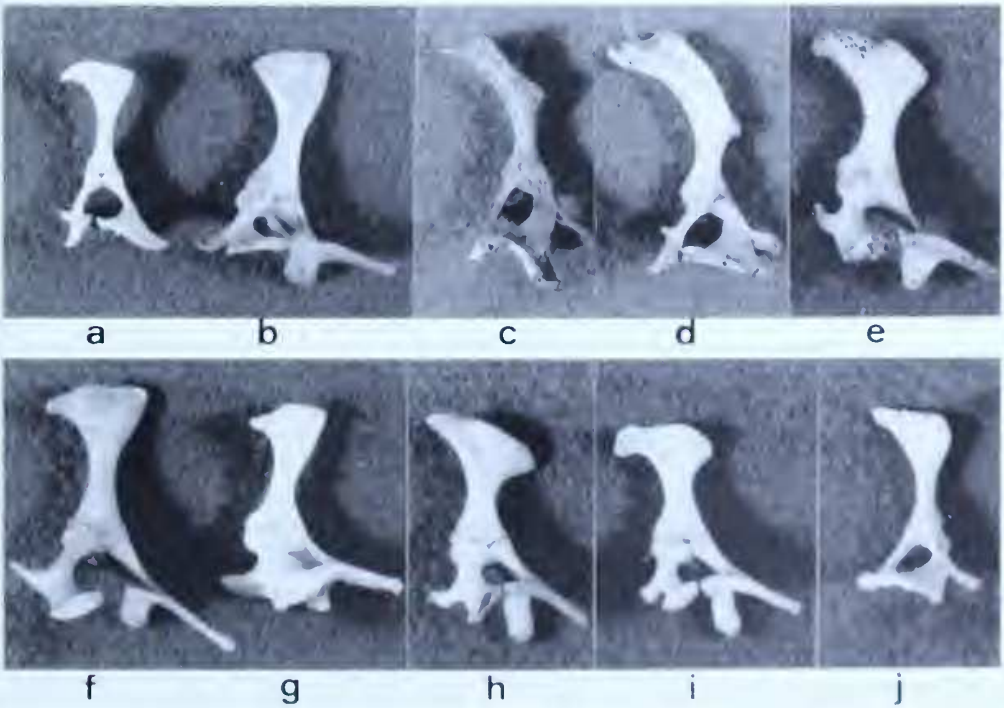


FIG. 1. Medial views of pelvic girdles. Batagurinae: (a) *Chinemys reevesii*, (b) *Stigmochelys crassicollis*; Geoemydinae: (c) *Cistoclemmys flavomarginata*, (d) *C. pallidifrons*, (e) *Pyxidea mouhotii*, (f) *Mauremys japonica*, (g) *M. mutica mutica*, (h) *Cuora trifasciata*, (i) *Rhinoclemmys pulcherrima manni*, (j) *Geoemyda japonica*.



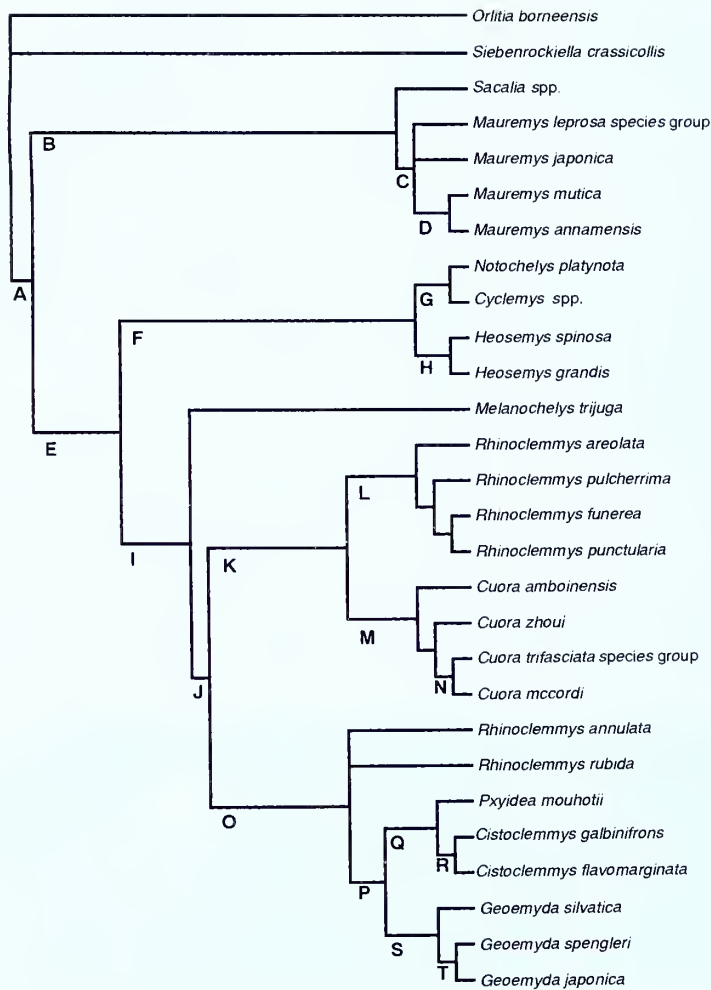


FIG. 3. Strict consensus cladogram of the subfamily Geoemydinae and its relatives.

previous empirical study dealing with a comparable number of OTUs (0.451 for 28 taxa: Sanderson and Donoghue, 1989), was much greater than that expected for random data (0.131 for 28 taxa; Klassen et al., 1991). Thus, we consider the monophyletic groups indicated in our results significantly realistic.

At the root of the Geoemydinae (Stem A), characters 1–27 and 31–35 were in the “0” state, whereas the characters 28–30 were “1”. We regarded these character states as ancestral within the Geoemydinae. Putative changes of character states in each major stem are given in Table 3.

Supposing that all character states in the outgroup represent primitive conditions, the monophyly of Geoemydinae (Stem A) was supported by three character states: character 1 (state 0), presence of frontal exposure on orbital rim; 12 (0), large foramen palatinum posterius with elliptic or oval shape; and 28 (2), axillary plastral buttress connected around the portion between peripherals and costals.

One synapomorphic character state, 31 (1) (smooth skin of posterior head), supported the *Mauremys*–*Sacalia* clade (Stem B), which we henceforth call the *Mauremys* group.

TABLE 3. Putative changes of character states in major stems of Geoemydinae. Letters denoting stems refer to those in Fig. 3.

Stem	Character	Change
A	1	1 to 0
	12	1 to 0
	28	1 to 2
B	31	0 to 1
C	14	0 to 1
	15	0 to 1
D	15	1 to 2
E	7	0 to 1
	8	0 to 1
	25	0 to 1
F	23	0 to 1
	32	0 to 1
G	21	0 to 1
	28	2 to 3
	30	1 to 2
H	6	0 to 1
	30	1 to 0
I	15	0 to 1
	18	0 to 2
J	9	0 to 1
	31	0 to 1
K	11	0 to 1
	14	0 to 2
	15	1 to 2
L	8	1 to 0
	9	1 to 0
M	19	0 to 1
	21	0 to 1
	28	2 to 3
	29	2 to 3
N	16	0 to 1
O	9	1 to 2
	13	0 to 1
	20	0 to 1
P	2	0 to 2
	3	0 to 1
	4	0 to 1
	5	0 to 1
	12	0 to 1

Q	24	0 to 1
	27	0 to 1
	15	1 to 0
	21	0 to 1
	28	2 to 3
R	29	2 to 3
	21	1 to 2
	22	0 to 2
	24	1 to 0
S	26	0 to 1
	34	0 to 1
	8	1 to 0
	10	0 to 1
	17	0 to 1
T	18	2 to 1
	33	0 to 1
	3	1 to 2
	15	1 to 2
	23	0 to 1

The genus *Mauremys* (Stem C) was supported by two character states: 14 (1), maxilla sometimes contacting vomer; and 15 (1), foramen praepalatinum sometimes opening within premaxilla. Autapomorphy of *Sacalia* was not detected. The *M. annamensis*-*M. mutica* clade (Stem D) was supported by 15 (2), foramen praepalatinum opening within premaxilla.

Stem E, henceforth referred to as the *Geoemyda* group, was supported by three synapomorphic character states: 7 (1), absence of the squamosal-quadratojugal contact; 8 (1), absence of the jugal-quadratojugal contact; and 25 (1), anterior neurals with shorter posterior sides. The former two character states are seemingly associated with the reduction of the quadratojugal. The state of the third character was constant within the group except for *Notochelys*.

The *Notochelys*-*Cyclemys*-*Heosemys* clade (Stem F) was supported by two synapomorphic character states: 23 (1), strong serration at posterior margin of carapace; and 32 (1), presence of radiated

markings on plastron. The *Notochelys-Cyclemys* clade (Stem G) was supported by three synapomorphic character states: 21 (1), plastral hinge not closing without gap; 28 (3), very weak axillary plastral buttress; and 30 (2), internal choanae usually with a small papillia. Monophyly of *Heosemys* (Stem H) was supported by two synapomorphic character states: 6 (1), loss of quadratojugal; and 30 (0), internal choanae without ridge, flap, or papillae. The latter was unique among the geoemydines. *Heosemys* was the sister group of the *Notochelys-Cyclemys* clade.

Stem I was supported by two synapomorphic character states: 15 (1), foramen praepalatinum sometimes opening within premaxilla; and 18 (2), processus trochlearis oticum mainly formed by the quadrate. Stem J was supported by two synapomorphic character states, 9 (1: usually flat jaw beak) and 31 (1: smooth posterior head skin), whereas *M. trijuga* had one autoapomorphic character state, 24 (1: three prominent keels).

*Rhinoclemmys* was shown to be polyphyletic, consisting of two groups, *Rhinoclemmys* A (*areolata*, *funerea*, *punctularia* and *pulcherrima*) and *Rhinoclemmys* B (*annulata* and *rubida*). The *Rhinoclemmys* A-*Cuora* clade (Stem K) was supported by three character states: 11 (1), very weak serration of upper labial margin; 14 (2), absence of the maxilla-vomer contact; and 15 (2), location of foramen praepalatinum within premaxilla. Within this clade, monophyly of the *Rhinoclemmys* A (Stem L) was supported by two character states, 8 (0: the jugal-quadratojugal contact) and 9 (0: notched and hooked beak of upper jaw), whereas the *R. funerea*-*R. punctularia* clade was supported by a unique synapomorphic character state 35 (1: usual presence of small foramen on ventral maxilla). *Cuora* (Stem M) was further supported by four synapomorphic character states: 19 (1), quadrate participation into canalis cavernosum; 21 (1), presence of

both plastral hinge and gap between closed shells; 28 (3), very weak axillary plastral buttress; and 29 (3), very weak inguinal plastral buttress. The *Cuora trifasciata* species group-*Cu. mccordi* clade (Stem N) was supported by a unique character state: 16 (1), prefrontal notched at posterior orbital margin.

Although there were no synapomorphies uniting the *Rhinoclemmys* B, the *Rhinoclemmys* B-*Cistoclemmys*-*Pyxidea*-*Geoemyda* clade (Stem O) was supported by three character states: 9 (2), unnotched and hooked upper jaw beak; 13 (1), anteromedial portion of triturating surface expanding medially; and 20 (1), reduction of hyoid apparatus.

Monophyly of the *Cistoclemmys*-*Pyxidea*-*Geoemyda* clade (Stem P) was supported by seven synapomorphic character states, 3 (1), foramen nervi vidiani located anteroventrally or laterally to anteroventral part of processus inferior parietalis; 4 (1), medial process of jugal with small tip; 27 (1), strong reduction or loss of cloacal bursae; 2 (2), strong ventral convergence of cranial cavity; 5 (1), usual absence of the jugal-pterygoid contact; 12 (1), small and round foramen palatinum posterius; and 24 (1), three prominent keels on carapace. The former three were unique among geoemydines. The *Cistoclemmys*-*Pyxidea* clade (Stem Q) was monophyletic on the basis of four character states: 15 (0), foramen praepalatinum located between premaxilla and vomer; 21 (1), presence of plastral hinge; 28 (3), very weak axillary plastral buttress; and 29 (3), very weak inguinal plastral buttress. Validity of *Cistoclemmys* (Stem R) was supported by five synapomorphic character states: 21 (2), plastral hinge closing shell without gap; 22 (2), absence of anal notch of plastron; 24 (0), usual absence of lateral keels on carapace; 26 (1), presence of sutures between lateral sides of seventh and eighth pleurals; and 34 (1), very long anterodorsal portion of iliac blade (unique in geoemydines, Fig. 1c, d).



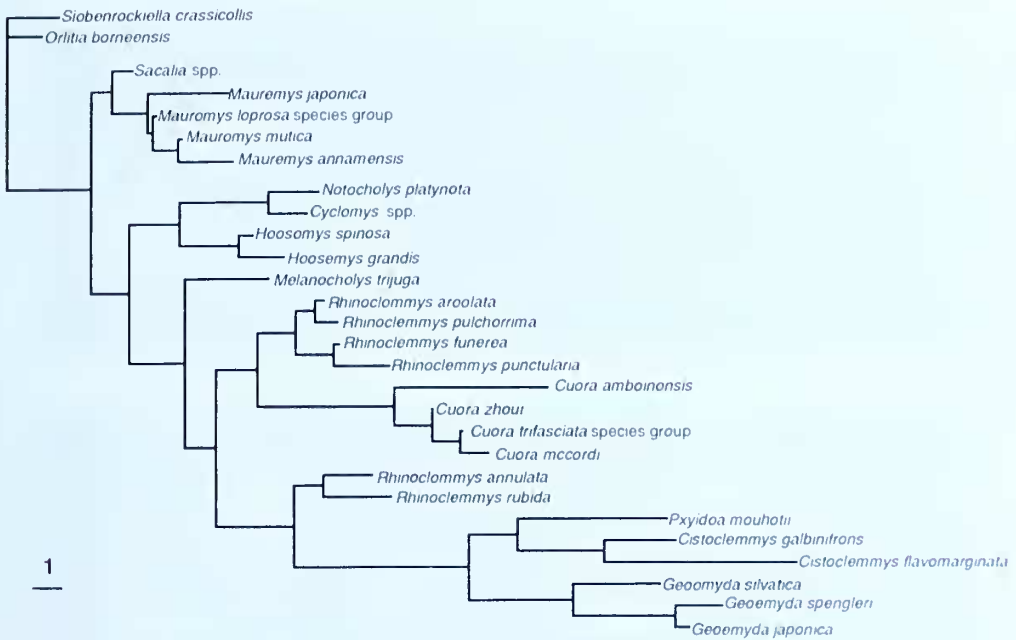


FIG. 4. Phylogram by neighbor-joining method of the subfamily Geoemydinae and its relatives.

*Pxyidea* had two autoapomorphic character states: 23 (1), strong serration of posterior carapace margin; and 31 (1), posterior head skin subdivided into small scales. Monophyly of *Geoemyda* (Stem S) was supported by five character states: 10 (1), ventromedial meeting of maxillae; 33 (1), entoplastron separated from gulo-humeral seam; 8 (0), presence of the jugal-quadratojugal contact; 17 (1), very weak maxilla-pterygoid contact; and 18 (1) processus trochlearis oticum formed with prootic and quadrate. The former two character states were unique in the Bataguridae. In addition, the *G. spengleri*-*G. japonica* clade (Stem T) was supported by three synapomorphic character states: 3 (2), foramen nervi vidiani sometimes located on pterygoid; 15 (2), foramen praepalatium opening within premaxilla; and 23 (1), strong serration at posterior carapace margin. The first was unique within the Bataguridae.

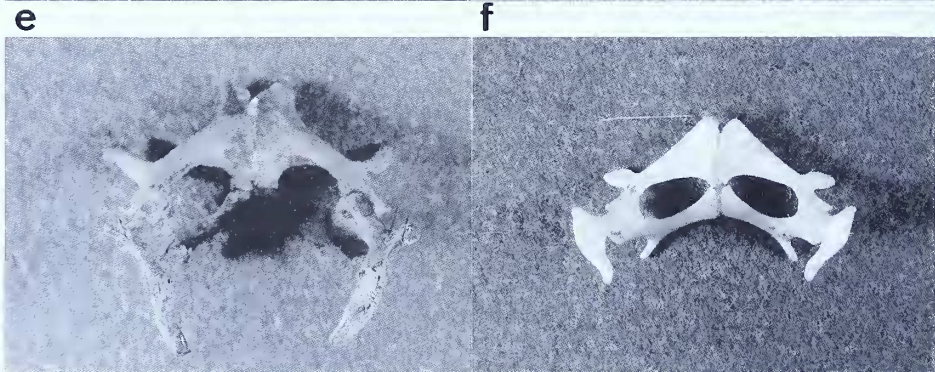
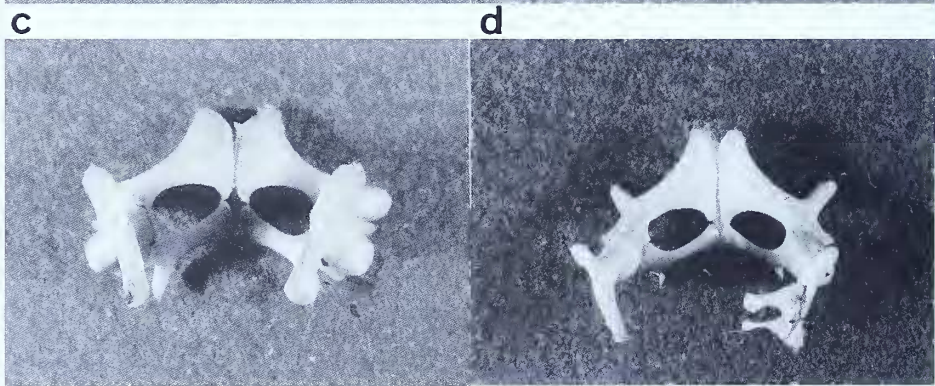
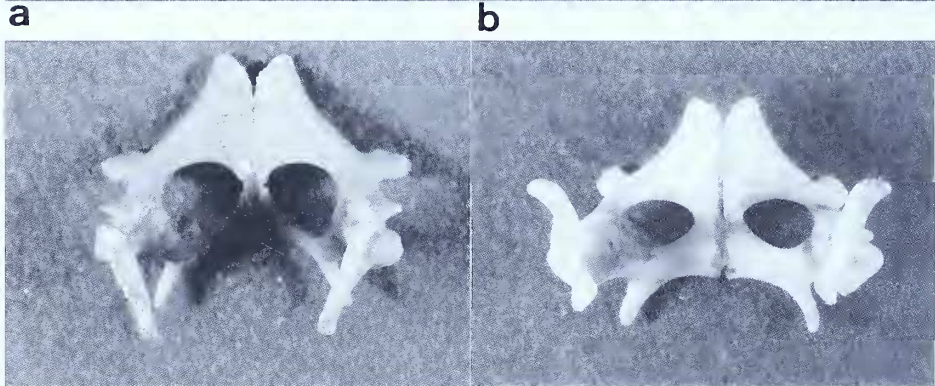
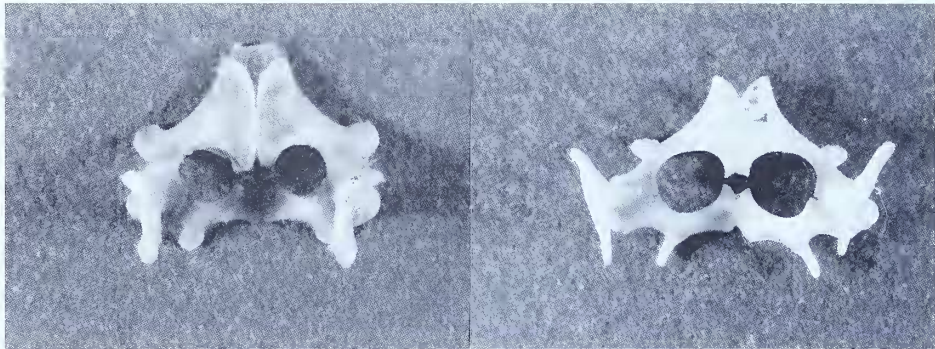
The phylogram, obtained by the neighbor-joining (NJ) method using an absolute distance matrix is shown in Fig. 4. This

phylogram is largely identical in topology with the strict consensus tree from the parsimony analysis (Fig. 3), and thus is interpreted as supporting the validity of the latter. One of the differences between the strict consensus tree and the NJ phylogram lay in the relationships within the *Rhinoclemmys* A. In the latter tree, *R. pulcherrima* was united not with the *R. funerea*-*R. punctulata* group but with *R. areolata*. Another difference was in the relationships among *R. annulata*, *R. rubida*, and the *Cistoclemmys*-*Pxyidea*-*Geoemyda* group. In the NJ phylogram, *R. annulata* and *R. rubida* were united, collectively constituting the first outgroup to the *Cistoclemmys*-*Pxyidea*-*Geoemyda* group.

DISCUSSION

Monophyly of the Bataguridae

Based on the analyses of morphological and mitochondrial DNA characters for major testudine taxa including one batagurine, one geoemydine, three emydid, and one testudinid genera, Shaffer et al. (1997)



**a** **b**  
**c** **d**  
**e** **f**  
**g** **h**



argued that both Bataguridae and Emydidae are probably monophyletic, and that the latter is the sister group of a clade consisting of the former and the Testudinidae. Recently we also found states of two morphological characters (i.e., well developed foramina of axillary and inguinal musk ducts with penetration into the breast chamber, and anterolaterally flared iliac blade [Fig. 2]) that seemingly lend further support to the monophyly of the Bataguridae (Yasukawa, 1997; Hirayama, Yasukawa and Aoki, unpublished data), because they occur in most batagurid turtles but not in the Emydidae or Testudinidae. In our examinations, the former character state occurred in all batagurids exclusive of *Morenia*. Musk ducts and indistinct musk foramina also exist in some non-testudinoid families of turtles, such as the Chelydridae, Chelydidae, Kinosternidae, and Platysternidae, and their occurrence is thus likely to represent primitive conditions in the Testudines (Gaffney and Meylan, 1988). However, development of musk duct foramina to the point of reaching the breast chamber is a condition unique to the Bataguridae (Hirayama, Yasukawa and Aoki, unpublished data). On the other hand, an anterolaterally flared iliac blade was observed in all batagurid, but not in other turtles including those belonging to non-testudinoid families. We excluded these characters from our analyses, since these are obviously not informative for the inference of relationships among the geoemydines. However, the states of these characters are possibly synapomorphs of the Bataguridae. Thus, in the sections below we take an a priori assumption of the batagurid monophyly.

### Monophyly of the Geoemydinae

McDowell (1964) referred to two character states as discriminating Geoemydinae from Batagurinae—narrow and flat triturating surfaces, and reduction or absence of the quadratojugal. The former probably represents a primitive condition of the Testudinoidea (Hirayama, 1984; Gaffney and Meylan, 1988). In this study, the latter condition is observed in the *Geoemyda* group exclusive of *G. spengleri*. Because the *Mauremys* group had a relatively large quadratojugal as in *Kachuga*, *Ocadia*, *Odsrlitia*, and *Siebenrockiella*, it seems to be more appropriate to consider the reduction or absence of the quadratojugal as a characteristic of the *Geoemyda* group rather than as a synapomorph of the Geoemydinae.

Hirayama (1984) considered that the subdivision of the foramen nervi trigeminalis, observed in more than 40% of the specimens examined for each geoemydine species, is a synapomorph of the Geoemydinae besides the loss or reduction of the quadratojugal. However, Gaffney and Meylan (1988) were concerned about such an inconsistent occurrence of the former character state, and argued that its use at this level was dubious. Our additional observations also confirmed the remarkable variability of this character at the intraspecific level (Yasukawa, unpublished observation). Therefore, we did not include this character in our phylogenetic analyses. Although Gaffney and Meylan (1988) regarded the loss or reduction of the quadratojugal as "relatively consistent" in geoemydines, this character state turned out to be confined to the *Geoemyda* group alone (see above).

Our analyses yielded states of three characters as possibly supporting monophyly of

FIG. 2. Dorsal views of pelvic girdles. Emydidae: (a) *Trachemys scripta elegans*, Batagurinae: (b) *Chinemys reevesii*; Geoemydinae: (c) *Mauremys japonica*, (d) *M. mutica mutica*, (e) *Cuora trifasciata*, (f) *Rhinoclemmys pulcherrima munn*, (g) *Cistoclemmys flavomarginata flavomarginata*, (h) *Geoemyda japonica*.



TABLE 4. Classifications of geoemydine turtles of the family Bataguridae, derived from results of this study. “\*”: species not examined; “?”: species of dubious generic allocation.

Testudinoidea		
Testudinidae		
Emydidae		
Bataguridae		
Batagurinae		
Geoemydinae		
Geoemyda group	11 genera	34 species
Genus <i>Chelopus</i>		2 species
<i>C. annulatus</i>		
<i>C. rubidus</i>		
Genus <i>Cistoclemmys</i>		2 species
<i>C. flavomarginata</i>		
<i>C. galbinifrons</i>		
Genus <i>Cuora</i>		7 species
<i>C. amboinensis</i>		
<i>C. aurocapitata</i>		
<i>C. mccordi</i>		
<i>C. pani</i>		
<i>C. trifasciata</i>		
<i>C. yunnanensis*</i>		
<i>C. zhoui</i>		
Genus <i>Cyclenys</i>		4 species
<i>C. dentata</i>		
<i>C. oldhamii</i>		
<i>C. pulchristriata</i>		
<i>C. tcheponensis</i>		
Genus <i>Geoemyda</i>		4 species
<i>G. japonica</i>		
<i>G. silvatica</i>		
<i>G. spengleri</i>		
? <i>G. leytenis*</i>		
Genus <i>Heosemys</i>		3 species
<i>H. depressa*</i>		
<i>H. grandis</i>		
<i>H. spinosa</i>		
Genus <i>Leucocephalon</i>		1 species
<i>L. ynwonoi*</i>		
Genus <i>Melanochelys</i>		2 species
<i>M. tricarinata*</i>		
<i>M. trijuga</i>		

Genus <i>Notochelys</i>	1 species
<i>N. platynota</i>	
Genus <i>Pyxidea</i>	1 species
<i>P. mouhotii</i>	
Genus <i>Rhinoclemmys</i>	7 species
<i>R. areolata</i>	
<i>R. diademata</i> *	
<i>R. funerea</i>	
<i>R. melanosterna</i> *	
<i>R. nasuta</i> *	
<i>R. pulcherrima</i>	
<i>R. punctularia</i>	
Mauremys group	2 genera 11 species
Genus <i>Mauremys</i>	8 species
<i>M. annamensis</i>	
<i>M. caspica</i>	
<i>M. iversoni</i> *	
<i>M. japonica</i>	
<i>M. leprosa</i>	
<i>M. mutica</i>	
? <i>M. pritchardi</i> *	
<i>M. rivulata</i>	
Genus <i>Sacalia</i>	3 species
<i>S. bealei</i>	
<i>S. pseudocellata</i> *	
<i>S. quadriocellata</i>	

the Geoemydinae: 1 (0), presence of frontal exposure on orbital rim; 12 (0), large and elongated foramen palatinum posterius; and 28 (2), axillary plastral buttress connected around the portion between peripherals and costals. Of these, however, the first and the third were also observed in various species of the Batagurinae (Table 1), Emydidae, and Testudinidae (Gaffney, 1979; Yasukawa and Hirayama, unpublished data), and thus seemingly represent primitive conditions of the Testudinoidea. The second was observed in all geoemydines except for the *Cistoclemmys*-*Pyxidea*-*Geoemyda* clade and thus may be a synapomorph of the subfamily. However, we failed to determine whether this state represents a derived or primitive condition,

because the character is highly variable within the Testudinoidea (Gaffney and Meylan, 1988; Yasukawa, unpublished data), and is also seen in Mesozoic primitive testudinoids such as *Mongolemys* (Hirayama, unpublished data).

There are no synapomorphs clearly supporting the monophyly of Geoemydinae. The character states shared by most members of this subfamily largely represent primitive conditions in the Bataguridae (Hirayama, 1984; Table 1). This may suggest the paraphyletic nature of the Geoemydinae as an assemblage of primitive stocks of the Bataguridae. Nevertheless, because we could also detect no synapomorphs supporting sister group relationship with the Batagurinae of any particular clade within the Geoemydinae, this problem remains to be readdressed on the basis of additional data. In consideration of taxonomic stability, we propose to temporarily retain the recognition of the subfamily Geoemydinae as a "metataxon", for which no character evidence supports or negates the monophyly (Gauthier et al., 1988).

Our analyses revealed that the Geoemydinae consists of the *Mauremys* and the *Geoemyda* groups. In the following subsections, we discuss the phylogeny within each of these groups. We also propose several modifications to the classification by David (1994) (Table 4) on the basis of evolutionary relationships revealed in this study.

#### *Mauremys* group

The results of this study may support the monophyly of the *Mauremys* group as consisting of *Mauremys* and *Sacalia* with one synapomorph (31 [1], smooth skin of the posterior head). Even so, however, this character state was also observed in Stem J except for *Geoemyda sylvatica* and *Praxidea*. This suggests that 31 (1) has evolved more than one time in the Geoemydinae, and reduces its value as evidence for monophyly of the *Mauremys* group. Other character

states exhibited by *Mauremys* and *Sacalia* seem to mostly represent primitive conditions of the Geoemydinae (Table 1), or of the whole family Bataguridae (Hirayama, 1984). Thus, the *Mauremys* group may be referred to as the primitive stock of this family.

Monophyly of the genus *Mauremys* was supported by two character states, 14 (1) and 15 (1), while *Sacalia* exhibited no autapomorphs in our parsimony analyses. McDowell (1964) suggested that *Sacalia* is discriminated from *Mauremys* in four character states. Of these, however, only one (a few very large scutes without intervening granules on forearms) is a possible synapomorph of the *Sacalia* species. Although we did not employ scutellation of the forearm in the phylogenetic analyses due to its extensive intrageneric variation in the *Geoemyda* group, we confirmed the unique state mentioned above in this character in *Sacalia*. Considering it as an autapomorph of *Sacalia*, we regard both *Mauremys* and *Sacalia* as valid.

#### *Geoemyda* group

In our results, the monophyly of the *Geoemyda* group is supported by three character states, absence of the squamosal-quadratojugal contact (7 [1]), absence of the jugal-quadratojugal contact (8 [1]), and anterior neurals with shorter posterior sides (25 [1]). Of these, 25 (1) was constant within the *Geoemyda* group exclusive of *Notochelys*, in which the anterior neurals had shorter anterior sides like those in the *Mauremys* group and most batagurines. Hirayama (1984) depicted a sister group relationship between *Sacalia* and *Notochelys* as supported by jugal-parietal contact, and distinctly widened first vertebral which sometimes reaches the second marginal. The present study revealed that the jugal is close to the parietal but separated from it in *Notochelys*, while the two make weak contact in *Sacalia*. The first vertebral was widened and usually reached the second

marginal in *Mauremys japonica*, the *M. leprosa* species-group, *Sacalia*, and sometimes in *Notochelys*, *M. annamensis*, *M. mutica*, the *Cuora trifasciata* species-group, *Cu. zhoui*, and *Melanochelys*. Thus, it is obviously inadequate to use these characters to unite *Sacalia* and *Notochelys*. In the present analyses, the *Notochelys*-*Cyclemys* clade is supported by three synapomorphic character states, and we thus consider this relationship to be far more likely than the *Notochelys*-*Sacalia* monophyly.

Except for the position of *Notochelys* (see above), our results largely support Hirayama's (1984) hypothesis in that they also suggest: polyphyly of *Cuora* (sensu lato) and validity of *Cistoclemmys*; close relationships among *Cistoclemmys*, *Pyxidea* and *Geoemyda*; and polyphyly of *Rhinoclemmys*. Sites et al. (1984), on the basis of the analysis of allozymic variation among 22 batagurid species, suggested that *Cuora* and *Cistoclemmys* are most closely related to each other. This has been one of the major reasons to regard *Cistoclemmys* as a junior synonym of *Cuora* (e.g., Ernst and Barbour, 1989; McCord and Iverson, 1991; Iverson, 1992). However, Sites et al. (1984) examined very small numbers of individuals for most species. The number of loci examined in that study was also very small. Our results showed that *Cistoclemmys* is related more closely to *Pyxidea* and *Geoemyda* than to *Cuora*, although *Cistoclemmys*, *Pyxidea*, and *Geoemyda* are well differentiated from each other (Fig. 4). Based on the external comparisons of subspecies of *Cistoclemmys galbinifrons* and *Pyxidea*, Fritz and Obst (1997) concluded that *Ci. g. serrata* is a distinct species which narrows the gap between *Cuora* (sensu lato) and *Pyxidea*. They doubted the validity of both *Cistoclemmys* and *Pyxidea*. However, the number of specimens of *Ci. g. serrata* examined by them was very small. Moreover, they did not examine internal characters, in which

we did find a number of remarkable differences among *Cistoclemmys*, *Cuora*, and *Pyxidea*. We thus consider the three genera to be valid.

The results of this study confirmed the polyphyly of *Rhinoclemmys* as proposed by Hirayama (1984), because they divided *Rhinoclemmys* into two groups belonging to different clades. Of these, *Rhinoclemmys* A consisted of two aquatic species, *punctularia* and *funerea*, and two terrestrial species, *areolata* and *pulcherrima*. *Rhinoclemmys* B, on the other hand, consisted of two terrestrial species with unnotched, hooked beaks, *annulata* and *rubida*, that were not united into a monophyletic group by the parsimonious analysis, but did constitute a single unit in the NJ phylogram. We thus discuss the relationship of these two *Rhinoclemmys* B species below.

Based exclusively on the coloration and the relative depth of the shell, Ernst (1978) demonstrated that *Rhinoclemmys* (as *Callopsis*) can be divided into three groups, the *pulcherrima*-*rubida* group, *punctularia* group (as consisting of *R. punctularia*, *R. annulata*, *R. diademata*, *R. funerea*, *R. melanosterna*, and *R. nasuta*), and *R. areolata*. This grouping substantially contradicts our results, especially in the positions of *R. annulata*, *R. pulcherrima*, and *R. rubida*. Considering the remarkable intersubspecific variation in those characters in both *R. pulcherrima* and *R. rubida* (Pritchard and Trebbau, 1984; Ernst and Barbour, 1989), the grouping proposed by Ernst (1978) is dubious.

Sites et al. (1981), in the assessment of allozymic variation among *R. areolata*, *R. funerea*, *R. pulcherrima*, *R. punctularia*, and *R. rubida*, suggested close affinity among *R. areolata*, *R. punctularia*, and *R. funerea*, and distinct differentiation among the *areolata*-*punctularia*-*funerea* assemblage, *R. pulcherrima*, and *R. rubida*. Our results are in accord with those of Sites et al. (1981) in showing close relationship



among *R. punctularia*, *R. funerea*, and *R. areolata*, but contradict the latter in showing the sole divergence of *R. rubida*. Because the results of Sites et al. (1981) were derived from analyses of a relatively small number of loci for very small samples, we consider that our results more successfully reflect the phylogeny of *Rhinoclemmys*.

The type species of *Rhinoclemmys* Fitzinger, 1835, is *Testudo dorsata* Schoepff, 1801, which is a junior synonym of *R. punctularia* (see Iverson, 1992). Therefore, *punctularia* and its relatives (*areolata*, *funerea*, and *pulcherrima*) should be retained under *Rhinoclemmys*, while *rubida* (type species of *Chelopus*) and *annulata* should be moved to the resurrected genus *Chelopus* Cope, 1870, which was formerly regarded as a junior synonym of *Rhinoclemmys* (see Wermuth and Mertens, 1977).

#### *Parallel evolution of plastral hinge*

Within the Bataguridae, a kinetic plastron equipped with a hinge between the pectoral and abdominal was observed in five geoemydine genera, *Cistoclemmys*, *Cuora*, *Cyclemys*, *Notochelys*, and *Pyxidea*. Bramble (1974) demonstrated distinct differences in shell-closing mechanism between emydid box turtles and batagurid box turtles. He argued that in the Geoemydinae the plastral hinge had evolved two times, in the common ancestor of *Cistoclemmys*, *Cuora*, *Cyclemys*, and *Pyxidea*, and in *Notochelys*. In addition, he noted that *Heosemys* had a more developed musculus testoscapularis (a muscle element associated with the closure of the anterior plastral lobe in the batagurid box turtles; Bramble, 1974) than the other geoemydines lacking a plastral hinge. He thus suspected the derivation of *Cistoclemmys*, *Cuora*, *Cyclemys*, and *Pyxidea* from a common *Heosemys*-like ancestor, and, on the basis of this consideration, united the five genera in the *Heosemys* group. However, our study showed

no distinct differences in the degree of development of m. testoscapularis between *Heosemys* and other "non-box" geoemydines (character 21). Additionally, we did not find any character to support monophyly of the *Heosemys* group, or of an assemblage of *Cistoclemmys*, *Cuora*, *Cyclemys*, and *Pyxidea*. We thus consider Bramble's (1974) grouping as unnatural.

Bramble (1974) also suggested that plastral kinesis of *Notochelys* arose apart from the *Heosemys* group. But he hardly mentioned the difference in shell-closing mechanism between *Notochelys* and the other batagurid box turtles. In adult living specimens, both anterior and posterior plastral lobes of *Notochelys* are as movable as those of *Cyclemys* but less movable than those of *Cistoclemmys*, *Cuora*, and *Pyxidea* (Yasukawa, unpublished data). Both *Cyclemys* and *Notochelys* have no hinge in juveniles, while the other three genera have a weak hinge even in juveniles (Yasukawa, unpublished data). In contrast, the very long anterodorsal portion of the iliac blade, a condition unique to the batagurids (character state 34 [1]; Fig. 1c, d), was observed only in *Cistoclemmys*. The shape of the iliac blade appears to be associated with the closure of the posterior plastral lobe (Bramble, 1974). We thus suspect that the most prominent difference in shell-closing mechanism exists between *Cistoclemmys* and the other geoemydine box turtles, not between *Notochelys* and the others. In the Geoemydinae, the plastral hinge seems to have actually evolved three times—in the *Notochelys*-*Cyclemys* clade (Stem G), *Cuora* (Stem M), and the *Pyxidea*-*Cistoclemmys* clade (Stem Q).

In adult females of some batagurids lacking the plastral hinge, the bony connection between the hypoplastron and carapace is replaced by a ligamentous connection. Such plastral kinesis, sometimes called sexually dimorphic plastral kinesis, is probably an adaptation for the passage of relatively large eggs which otherwise could not



pass through the posterior opening between carapace and plastron (Waagen, 1984; Moll, 1985). Sexually dimorphic plastral kinesis is present in *Geoemyda japonica*, *G. spengleri* (see Yasukawa et al. [1992]), *G. silvatica* (see Moll et al. [1986]), *Heosemys grandis* (Yasukawa unpublished data), *H. spinosa* (see Moll [1985]), *Melanochelys tricarinata* (see Waagen [1984]), and *Rhinoclemmys* spp. (see Pritchard and Trebbau [1984]). Therefore, all members of the *Geoemyda* group exclusive of *Melanochelys trijuga* actually show plastral kinesis at least in adult females. Considering its sporadic emergences on the phylogenetic tree of the *Geoemyda* group, it is probable that sexually dimorphic plastral kinesis represents a primitive condition in this group.

#### Taxonomic notes

Based on the strong plastral buttresses in *Mauremys annamensis*, Savage (1953) revalidated the monotypic genus *Annamemys* Bourret 1939, for this species. He also suggested its close affinity to several batagurines with strong plastral buttresses, such as *Batagur*, *Callagur*, *Hardella*, and *Kachuga*. On the other hand, Iverson and McCord (1994), in the analyses of morphometric variation in the East Asian *Mauromys*, regarded *annamensis* as the closest relative of *M. mutica*, and synonymized *Annameinys* with *Mauremys* again. The present study showed that the buttress of *M. annamensis* is stronger than that of other geoemydines, but much less developed than that of the above-mentioned batagurines (see comments for characters 28 and 29). Except for the buttress, this species shared most character states with *M. mutica*, supporting Iverson and McCord's (1994) account (Table 1). Assignment of this species to the genus *Mauremys* was also supported by a recent mitochondrial DNA study, which, however, suggested the closest affinity of *M. annamensis* with *M. iversoni* rather than with *M. mutica* (Honda et al., in press).

The NJ phylogram, while supporting the *aurocapitata-pani-trifasciata-mccordi-zhoui* assemblage, showed that *Cu. amboinensis*, the type species of the genus, is highly differentiated from the other congeners. Such a relationship was also supported by the cladogram as well. However, we found no character states definitely uniting the five species. Therefore, we do not further divide this genus.

Of the currently recognized species of *Cuora* (sensu lato), *Cu. yunnanensis* from Yunnan, China, was not examined in our study. Examining all syntypes (=all available specimens since the description by Boulenger [1906]) of this rare species, Ernst (1988) demonstrated a close relationship of *Cu. yunnanensis* with *Cu. trifasciata*. McCord and Iverson (1991) also suggested a close affinity of *Cu. yunnanensis* with *Cu. trifasciata*, as well as with *Cu. pani* and *Cu. aurocapitata* on the basis of morphometric comparisons among all extant *Cuora* (sensu lato). Therefore, we tentatively retain this species in the genus *Cuora* (sensu stricto).

*Geoemyda silvatica* is an enigmatic species endemic to the Western Ghats of southwestern India (Das, 1991; 2001). Its generic allocation has been in dispute. Some authors assigned this species to *Geoemyda*, while others assigned it to *Heosemys* (see the *Geoemyda* subsection in "Materials and Methods"). Such a taxonomic confusion is probably attributable to the paucity of studies directly comparing specimens of *G. japonica*, *G. silvatica*, and *G. spengleri*. We examined representatives of all these species in detail, and our results strongly suggest the monophyly of the three species and the validity of the *G. japonica-G. spengleri* clade.

Of the currently recognized species of *Rhinoclemmys* (sensu lato) *R. inelanosterna*, *R. diadenata*, and *R. nasuta* were not examined. They were once treated as subspecies of *R. punctularia*, and then

were elevated to full species (Pritchard, 1979; Pritchard and Trebbau, 1984; David, 1994). Like *R. punctularia* and *R. funerea*, all of the three species are aquatic and have a shallowly notched upper beak (Ernst and Barbour, 1989). In addition, a small foramen on the ventral maxilla, which is suggested to be a unique synapomorphy of the *R. punctularia*-*R. funerea* clade (35 [1]), was recognized in juvenile specimens of *R. melanosterna* and *R. diademata* (Hirayama, unpublished data). We thus tentatively retain the three species in the genus *Rhinoclemmys* (sensu stricto).

#### *Direction of future studies on the geoemydine phylogeny*

In this study, we attempted as comprehensive an analysis as ever made for the phylogeny of the highly diversified subfamily Geoemydinae by best use of morphological information.

As a result, we established a best-fitting phylogenetic hypothesis at this level (Figs. 3 and 4), and accordingly suggested some changes in the classification of this subfamily (see above). Nevertheless, our analysis failed to resolve a number of ingroup relationships. Moreover, our results, as well as our presumption of the batagurine monophyly, substantially contradict the results of recent preliminary molecular studies on the batagurid phylogeny (e.g., Sites et al., 1984; Shaffer et al., 1997; Wu et al., 1998; McCord et al., 2000; Honda et al., in press). In the future, more comprehensive phylogenetic analyses of Testudinoidea using molecular data are desirable to test and revise, when necessary, the hypothesis and classification herein proposed.

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#### APPENDIX

*Specimens Examined.*—Catalogue numbers of specimens deposited in reptile collection of Kyoto University Museum,

turtles collections of Madras Crocodile Bank Trust, Biological collections of Teikyo Heisei University, and private collections of Ren Hirayama and P. C. H. Pritchard are preceded by KUZ R, MCBT, THUb, RH and PCHP, respectively. The other acronyms are those suggested by Leviton et al. (1985).

Geoemydinae: *Chelopus annulatus* (2 specimens) RH861–862; *C. rubidus* (1) RH331; *Cistoclemmys flavomarginata flavomarginata* (9) NSMT02087–02089, one unnumbered specimen of OMNH-R, KUZ R19561, 36752, RH; 53, 62–63, 430; *Ci. f. evelynae* (4) NSMT02090–02092, KUZ R36746; *Ci. galbinifrons* (7) KUZ R36745, 36757, 36763, RH736–737, 750–751; *Cuora amboinensis amboinensis* (2) KUZ R36704–36705; *Cu. a. kumaroma* (13) KUZ R19583–19584, 36763, RH34–36, 519–520, 596–600, *Cu. aurocapitata* (4) KUZ R36710, THUb13–14, RH915; *Cu. mccordi* (6) THUb21–22, RH935–936, 950, 981; *Cu. pani* (4) RH901–903, 987; *Cu. trifasciata* (5) KUZ R 36709, RH219–222; *Cu. zhoui* (4) KUZ R36706, 36711, RH868, 1001; *Cyclemys* spp. (11) KUZ R 36609, 36707–36708, RH134–139, 550–551; *Geomyda japonica* (13) NSMT02083–02086, OMNH-R333–3334, two unnumbered specimens of OPM, KUZ R36720–36721; RH480–482; *G. silvatica* (6) FMNH52515, four unnumbered specimens of MCBT, PCHP2725; *G. spengleri* (12) two unnumbered specimens of NSMT, USNM84992, KUZ R9994, 12630, 19399–19401, THUb15, RH847, 856, 857; *Heosemys grandis* (3) KUZ R19581, 36718, RH581; *H. spinosa* (4) KUZ R36757, RH185–186, 266–267; *Mauremys annamensis* (6) KUZ R36700, RH 936–939, THUb 9; *M.*

*caspica* (1), RH666; *M. japonica* (10) KUZ R19575–19580, 36712–36715; *M. leprosa* (2) RH453–454; *M. mutica kami* (5) KUZ R19524–19525, 19541, 19543–19545; *M. m. mutica* (6) KUZ R19509–19512, RH54, 194; *M. rivulata rivulata* (6) KUZ R36716, 36761, RH541–542, 888, 929–930; *Melanochelys trijuga* (10) KUZ R36718–36720, four unnumbered specimens of MCBT, RH238, 549, 557; *Notochelys platynota* (6) KUZ R36721–36722, RH858, 869, 961–962; *Pyxidea mouhotii* (5) KUZ R36723, RH240, 246–247, 269, 273; *Rhinoclemmys areolata* (2) RH654–656; *R. funerea* (3) 978, 985–986; *R. pulcherrima mani* (5) KUZ R36724, THUb17–19, RH835, 836; *R. punctularia* (4) 239, 248, 457, 510; *Sacalia bealei* (2) RH525–526; *S. quadriocellata* (2) KUZ R36725, RH709; *Sacalia* sp. (2: skeletal specimens not identified at the species level) RH308, 524. Batagurinae: *Batagur baska* (2) one unnumbered specimen of MCBT, RH 1002; *Callagur borneoensis* (3) KUZ R19560, RH287, THUb10; *Chinemys reevesii* (10) KUZ R 19591–19593, 36692–36698; *Geoclemys hamiltonii* (2) one unnumbered specimen of MCBT, RH920; *Hardella thurjii thurjii* (3) KUZ R 36699, 36701, THUb35; *Hieremys annandalii* (3) RH236, 587, 928; *Kachuga smithii smithii* (5) KUZ R 36759–36760, RH281, THUb49, 52, *Malayemys subtrijuga* (4) RH140–143, *Morenia petersi* (2) KUZ R 36702–36703, *Ocadia sinensis* (4) RH201–202, 340–341; *Orlitia borneensis* (1) RH871; *Siebenrockiella crassicollis* (5) KUZ R36762; RH116, 706–708.

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